

Update on Root Biology

Root Architecture and Plant Productivity¹

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Water and nutrient availability limit plant growth in all but a very few natural ecosystems. They limit yield in most agricultural ecosystems, and in the United States and other industrialized nations, intensive irrigation and fertilization have generated serious environmental problems. The acquisition of soil resources by plant root systems is therefore a subject of considerable interest in agriculture and ecology, as well as a complex and challenging problem in basic plant biology. Symbioses between roots and other organisms (notably mycorrhizas and N-fixing bacteria), modification of the rhizosphere through root exudates, and the uptake and transport characteristics of root axes are all important dimensions of this problem that are being actively researched by plant biologists. Another aspect of this problem that has received less attention, despite its probable importance, is root architecture. Recent methodological innovations present opportunities for improved understanding of the functional importance of root architecture in the efficient acquisition of soil resources and plant adaptation to suboptimal soil conditions. The purpose of this Update is to briefly summarize conceptual issues and recent developments in the study of root architecture and to propose a framework for understanding its physiological basis.

WHAT IS ROOT ARCHITECTURE?

The term “architecture” in reference to biological objects usually denotes the spatial configuration of some complex assemblage of subunits, with the implication that the overall configuration has some functional significance. The term “root architecture” has been used in various contexts to refer to distinct aspects of the shape of root systems. The following glossary more clearly delineates architecture from other terms:

Morphology. Root morphology refers to the surface features of a single root axis as an organ, including characteristics of the epidermis such as root hairs, root diameter, the root cap, the pattern of appearance of daughter roots, undulations of the root axis, and cortical senescence. Anatomical features of a root related to cell and tissue organization are not usually part of architectural considerations.

Topology. Root topology refers to how individual root axes are connected to each other through branching. As in math-

ematical usage, root topology is stable to deformation or rotation of the axes themselves and therefore is possible to measure on excavated root systems.

Distribution. Root distribution refers to the presence (rather than the orientation) of roots in a positional gradient or grid. Typically, studies of root distribution are concerned with root biomass or root length as a function of factors such as depth in the soil, distance from the stem, and position between neighboring plants. Measurement of root distribution in agricultural and natural plant communities often includes roots of more than one plant or more than one species.

Architecture. Root architecture refers to the spatial configuration of the root system, i.e. the explicit geometric deployment of root axes. Usually, studies of root architecture do not include fine structural details, such as root hairs, but are concerned with an entire root system or a large subset of the root system of an individual plant.

As a descriptor of multiple root axes, architecture is senior to topology and distribution, since if root architecture is known, both topology and distribution are also known, whereas neither topology nor distribution can be used to derive the other two descriptors. Accordingly, root topology and distribution are easier to measure than root architecture and are more commonly used in studies of root form.

Root architecture is generally quite complex. Figure 1 shows a geometric simulation of the architecture of a common bean seedling at 14 d of age. The common bean is typical of many herbaceous dicots in having a taproot and a crown of basal roots from which lateral roots emerge. Although this is a relatively simple architectural motif, the resulting object is quite complex after only 14 d of growth; root systems of mature plants are too complex to represent accurately in a figure. Root systems show considerable architectural variation among species (Fig. 2), among genotypes of a given species, and even within different parts of a single root system (e.g. diagram 9 of Fig. 2). The diversity and plasticity of root architecture are simultaneously a daunting methodological challenge and an intriguing aspect of the functional morphology of plants.

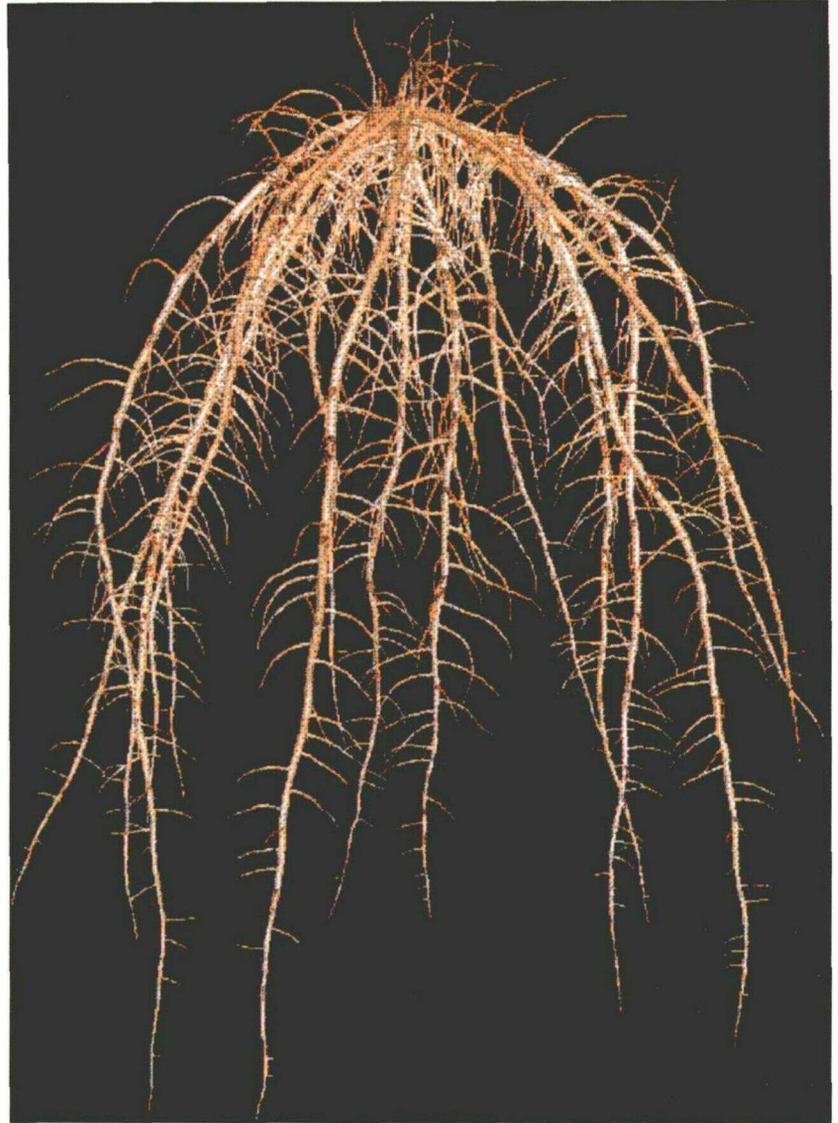
WHY IS ROOT ARCHITECTURE IMPORTANT IN PLANT PRODUCTIVITY?

Although there are no accurate quantitative estimates of the extent and importance of edaphic constraints to plant productivity, they must certainly be very substantial.

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Figure 1. Computer simulation of the root architecture of common bean, var *Carioca*, 14 d after planting. The simulation was carried out in the geometric modeling software SimRoot, using as inputs empirical data obtained in the field (Nielsen et al., 1994).



About one-third of the earth's land surface is arid, and there are very few areas, even in the humid tropics, that are not subject to periodic drought of sufficient duration to inhibit plant growth. Nutrient limitations are less well appreciated but may be equally important. Suboptimal availability of N and P is nearly universal, and acidity, salinity, and base imbalances are common in native soils.

The importance of root architecture in plant productivity stems from the fact that many soil resources are unevenly distributed, or are subject to localized depletion, so that the spatial deployment of the root system will in large measure determine the ability of a plant to exploit those resources. Patches of localized soil P availability may retain their boundaries within millimeters or centimeters over some years. Very strong gradients in temperature, oxygen status, water availability, pH, bulk density, and nutrient status commonly occur with soil depth over a scale of centimeters. Often such gradients present conflicting constraints and opportunities from the perspective of resource acquisition; for example, topsoils tend to be richer in nutrients

but also drier and more subject to temperature extremes than subsoils. The activities of soil animals such as earthworms and ants can create localized bonanzas of loose, fertile soil in horizons that may otherwise be resource poor. Root activity itself creates strong gradients in surrounding soil through, for example, the depletion of immobile nutrients such as P.

Spatial heterogeneity of nutrients is evident in the weathered Oxisols and Ultisols of the humid tropics, which are warm and moist throughout the soil profile but in which available P, Ca, and other mineral nutrients are concentrated in a thin surface layer. Desert Aridisols show pronounced spatial heterogeneity in water availability, both with depth and because of landscape drainage patterns. The Spodosols common to temperate coniferous forests have striking horizonation, with a black layer of acidic leaf litter over a white layer of leached sand, followed by an orange layer of clay and nutrient accumulation, all within 1 m or less of the soil surface. Temperate forest soils also experience dramatic seasonal fluctuations, as melting snow

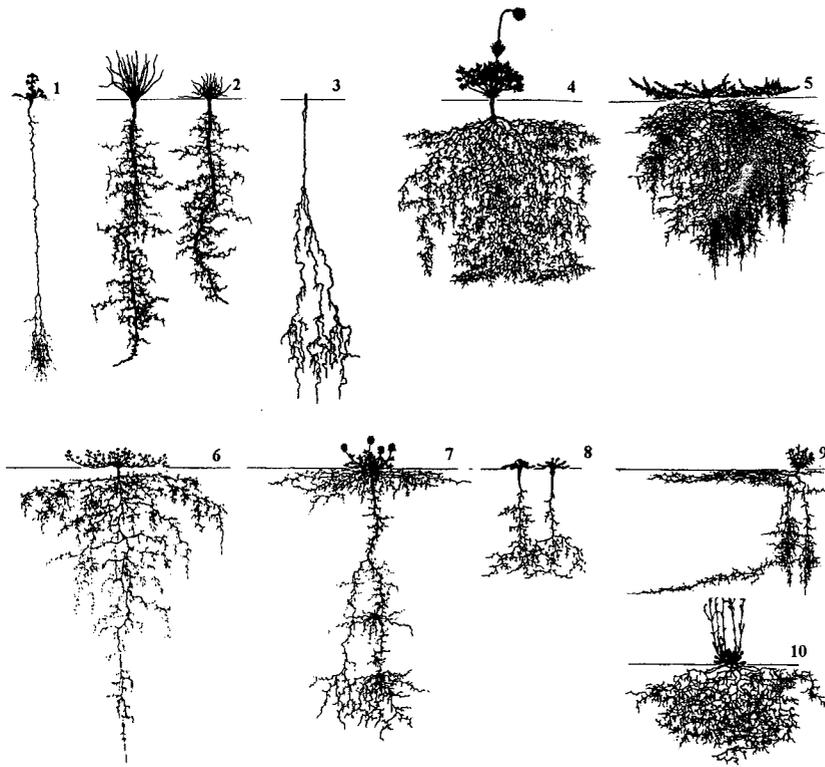


Figure 2. An example of variation in root architecture (as manifested in partial excavations) among diverse European dicots, from Kutschera and Lichtenegger (1992). 1, *Eryngium campestre*; 2, *Scorzonera villosa*; 3, *Chondrilla juncea*; 4, *Pulsatilla pratensis*; 5, *Genista germanica*; 6, *Trigonella balansae*; 7, *Trifolium trichocephalum*; 8, *Carum caucasicum*; 9, *Onosma arenarium*; 10, *Silene otites*.

in the spring flushes accumulated mobile nutrients such as nitrate through the soil. In this case roots must respond to a temporal pulse of resources before they are lost to ground water.

The pervasiveness of edaphic constraints and the heterogeneous availability of soil resources make soil exploration and colonization a challenging primary function in plant growth. Indeed, many reports document that the exploitation of soil resources through root activity may consume more than half of the available photosynthate in mature plants (Fogel, 1985). Given competing demands for internal plant resources for photosynthesis, support, defense, and reproduction, it is reasonable to expect that evolutionary pressures would have favored plants that directed root activity to exploit efficiently (i.e. with a favorable balance of resource investment versus resource acquisition) the heterogeneous distribution of soil resources. The architecture of a root system determines its exploration of distinct spatial domains in the soil, as well as its ability to respond dynamically to the localized availability of soil resources through meristematic activity, and its distribution of resource capture and transport functions (which are highly nonuniform within a root system). In addition to the relevance of root topology to soil exploration, Fitter (1991) has proposed that it has important implications for the construction cost of root systems, largely through consideration of the role of topology in determining the volume of root tissue required to support exploration of a given volume of soil. He has also proposed that topology influences the efficiency with which water and solutes can be conveyed to the shoots, because it deter-

mines the manner in which conducting elements are arrayed. The importance of root architecture in plant productivity therefore derives directly from the need to exploit a spatially heterogeneous environment, as well as economies of form and function inherent to the root system.

Indeed, root architecture has been linked with plant acquisition of water (see below) and, by extension, nutrients that move with water, as well as immobile (diffusion-limited) nutrients such as P (see below). The function of roots in mechanical support of the shoot is also determined by root architecture (Ennos and Fitter, 1992). An important ecological topic that has received less attention is how root architecture may influence root interactions with soil biota and soil processes by determining the biophysical environment of C fluxes and other plant-mediated processes (Wullschleger et al., 1994). The following two case studies illustrate the importance of root architecture in the productivity of plants in both agricultural and ecological contexts.

ROOT ARCHITECTURE IN AGRICULTURAL PRODUCTIVITY: THE CASE OF P EFFICIENCY IN BEAN

An example of the importance of root architecture in agricultural productivity is provided by the case of P efficiency in the common bean (*Phaseolus vulgaris* L.; summarized by Lynch and Beebe, 1995). P deficiency is a primary limitation to bean production in developing countries. Bean genotypes vary substantially in their adaptation to low-P soils, apparently because of differing ability to acquire P from the soil. Mechanisms of enhanced P acquisition may include soil P mobilization through root exudates

(such as phosphatases, organic acids, and protons), symbioses with vesicular-arbuscular mycorrhizas and other soil microbes, and enhanced root growth and activity. Studies of contrasting bean genotypes in diverse soils and media indicate that mobilization of specific soil P pools and interaction with specific soil organisms do not account for genetic differences in P efficiency (Yan et al., 1995a, 1995b). However, substantial genetic variation in the growth and architecture of bean root systems exists, and there is preliminary evidence that P-efficient genotypes have a vigorous, highly branched root system with a large number of apices (Lynch and van Beem, 1993). Theoretical studies with geometric models of bean root systems suggest that architectural differences could substantially influence the physiological efficiency of P acquisition, defined as C expended by the root in biomass deposition, respiration, and exudation, compared to P acquired by the root system (Fig. 3; Nielsen et al., 1994). This is significant, since growth analysis, simulation models, and C budgets of vegetative bean plants indicate that increased root C costs under P stress (because of a higher root/shoot ratio) may be an important component of reduced plant productivity (Lynch et al., 1991; Lynch and Beebe, 1995).

Roots of P-efficient bean plants also demonstrate high "plasticity," or the ability to sense and respond to localized changes in P availability. It has been known for some time that roots proliferate in zones of high nutrient availability (Nobbe, 1862); we have also observed stimulation of lateral root elongation in response to low P availability, in what may be interpreted as accelerated soil exploration. Bean roots change their geotropic curvature in response to low P availability, thereby changing the total volume of soil explored by basal roots (basal roots are the main lateral

branches from the hypocotyl in a dicot seedling), as well as the proportion of the root system in the topsoil, where P availability is typically higher than in the subsoil. The growth angle of basal roots 5 d after germination in low-P media is significantly correlated with P efficiency assessed in yield trials on low-P soils in the tropics, with genotypes having shallower roots being more P efficient. This sort of selective exploitation of specific soil domains could contribute significantly to root system efficiency by allocating C expenditures to portions of the environment with greatest P availability.

ROOT ARCHITECTURE IN ECOLOGICAL PRODUCTIVITY: THE CASE OF WATER ACQUISITION BY DESERT SUCCULENTS

Elegant work by Nobel and colleagues (summarized by Rundel and Nobel, 1991) provides compelling evidence for the importance of root architecture (or root distribution resulting from root architecture) in the productivity of desert plants. Water availability in desert environments varies greatly with soil depth and time. Work during the early part of the century established the existence of distinct architectural classes of desert root systems, with varying emphasis on deep taproots, shallow lateral roots, or generalized exploration of the soil profile (Cannon, 1911). These classes are apparently related to the growth strategies of the shoots. For example, deeply rooted phreatophytes can photosynthesize and grow in very dry conditions because they have access to deep water resources, whereas shallow-rooted perennials exploit brief seasonal rains but must tolerate long dry periods; cacti are an example of such species.

Nobel and colleagues used physiological analysis of root hydraulic properties, simulation modeling, and theories of cost/benefit optimization (i.e. applying microeconomic principles to plant resource allocation, as summarized by Bloom et al., 1985) to assess the functional significance of root architecture to the productivity of two succulent species. Root deployment in the soil and root hydraulic conductance were characterized, and this was used along with rainfall data and a model of water movement through the soil to simulate total water uptake in wet, average, and dry years. The model showed that the root distribution observed in the field was in fact the ideal distribution for water uptake in dry and average years, compared to other hypothetical distributions. It was demonstrated, using a similar approach but including the C "gain" of root water uptake by estimation of leaf water use efficiency, that the standing root biomass is nearly optimal from the point of view of C-gain optimization (i.e. additional root biomass would not have significantly enhanced net C gain) and that short-lived "rain roots" that appear after rain storms are economical "investments" by the plant despite their high C "cost."

METHODOLOGICAL CHALLENGES AND OPPORTUNITIES

The use of simulation models in both of the above examples highlights the need for creative approaches to the

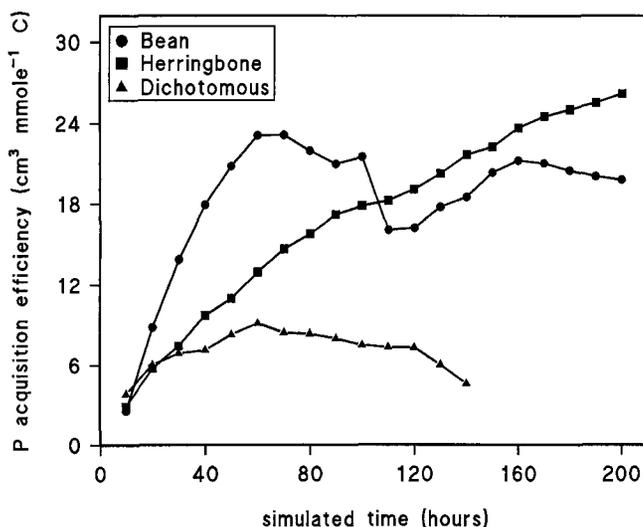


Figure 3. P acquisition efficiency (cm^3 soil depleted of P mmol^{-1} C expended by the root system) over time for three simulated root architectures: herringbone (a taproot with first-order lateral roots), dichotomous (with successive bifurcations of the root apices, resulting in many fine terminal roots and no central taproot), and a bean root system (based on empirical observations of actual bean roots, as shown in Fig. 1). From Nielsen et al. (1994).

study of root architecture. The reason we know relatively little about root architecture is that it is difficult to observe, quantify, and interpret. Roots grow in soil, an opaque medium from which they cannot be extricated or readily observed without introducing artifacts, destroying the native root architecture, or precluding subsequent analysis of the same individual. Root systems themselves are exceedingly complex structures, typically being composed of thousands of individual root axes that vary developmentally, physiologically, and morphologically. At present there are no satisfactory analytical frameworks or quantitative tools to describe or summarize this complexity when it is characterized. Furthermore, root growth and architecture are plastic and interact dynamically with a wide array of physical, chemical, and biological factors in the soil that vary in time and space.

These difficulties in analyzing the architecture of actual root systems make simulation modeling an attractive complementary approach. Simulation modeling has heuristic value in helping the modeler define relevant processes and interactions, in assessing the impact of single variables on system performance through sensitivity analysis, and in suggesting issues and hypotheses for experimentation (Wullschleger et al., 1994). Experimentation can help refine the model, which can then suggest further experimentation, in an iterative process that eventually may lead to a model of sufficient validity for use in predictive scenarios or as a module of more integrative models. Despite impressive recent progress in modeling root systems as dynamic geometric objects (e.g. Fig. 1), modeling the functional implications of root architecture is still in the stage of methodology development, and in some cases of suggesting experimental work, and is not yet predictive or fully validated (Lynch and Nielsen, 1995). As an aid to physiological research, simulation modeling has a very useful role in integrating information about specific processes or root axis responses into a complex three-dimensional context.

A kinematic approach to root axes, which allows the distinction of changes that occur along a root axis as a function of growth from those changes that occur independently of growth processes, has been very useful in addressing the spatial and temporal dynamics of root processes (Silk, 1984). Kinematics distinguishes local and convective changes of a measurable property; the local represents changes within a small particle (such as a cell or group of cells) as it matures, and the convective is associated with displacement of the particle from the root tip by root axis extension. Although kinematics have so far provided important insights into processes within single root axes (e.g. Spollen and Sharp, 1991), incorporation of kinematics into an architectural model, in which the root system is considered to be a population of root axes with specific kinematic characteristics, will provide useful physiological insights and will also suggest some efficient algorithms for simulation of developmental processes. Further physiological work is needed at high spatial resolution (perhaps 1 mm or less) before the potential of kinematics can be broadly realized, however.

A promising new technology permitting the noninvasive visualization of root architecture in soil is tomography, especially magnetic resonance imaging and x-ray computer-aided tomography (Anderson and Hopmans, 1994). These are particularly useful for the study of water flow in plant-soil systems, since water content and the status of H atoms in the sample can be distinguished. The availability of the technique for most root researchers is restricted, however, by limited access to suitable equipment and the substantial expertise and cost required to obtain satisfactory results. It is also difficult with present technology to image fine roots in soil volumes that do not restrict the growth of mature plants. As these technical difficulties are inevitably overcome, tomography will play an increasingly important role in the study of root architecture. It is important to note, however, that the visualization of root architecture in soil still presents a geometric object that is difficult to quantify, summarize, or interpret.

A relatively new approach to the quantification of root architecture is fractal geometry. Fractal geometry is a system of geometry that is more suited to the description of complex natural objects than is standard Euclidean geometry (Mandelbrot, 1983). A fractal is an object having a noninteger dimension, and root systems approximate fractal objects over a finite range of scales (Tatsumi et al., 1989). It is reasonable to hope that fractal geometry may provide quantitative summaries and functional insights into root architecture that have eluded researchers using Euclidean geometry (Berntson et al., 1995). For example, we have recently demonstrated that the fractal geometry of a root system in three spatial dimensions can be estimated from measurements of the fractal geometry in one and two spatial dimensions, such as might be measured from soil cores and exposed trenches (Nielsen and Lynch, 1994). If specific functional attributes can be linked to fractal geometry, fractal properties may be useful in plant breeding, as indices of below-ground functioning, etc. Fractal geometry may also provide useful perspectives on root-branching patterns.

An important conceptual issue in the analysis of root architecture is the quantification of the functional significance of any given architectural trait to the plant. The work of Nobel and colleagues noted above illustrates one fruitful approach to this problem: the use of an economic paradigm to develop "currencies" such as C through which quantitative cost/benefit analyses may be conducted. This approach certainly has heuristic value but is not without limitations, such as excessive emphasis on a few resources important in photosynthesis (notably water, C, and N) without regard to actual or multiple resource limitations encountered in the soil (see, for example, Lynch and González, 1993).

AN APPROACH TO THE PHYSIOLOGY OF ROOT ARCHITECTURE

A number of important issues concerning root architecture would benefit from physiological approaches, such as the precise role of specific architectural traits in improving plant performance under given conditions, how individual

traits of root axes are integrated into overall root system architecture, how root architectural traits sense and respond to environmental conditions, and what specific traits may be amenable to targeted genetic modification or tagging. At present, very little is known of the physiological basis for root architecture. In part this is because of the daunting complexity of the problem, but another obstacle is that root architecture is an aggregate characteristic that is generated by several distinct processes of root axes, only a few of which are understood from a physiological perspective. Root architecture is the result of (a) the extension growth of individual root axes, (b) the appearance of daughter roots along root axes, (c) the direction of root axis elongation (notably in response to gravity), (d) the senescence or mortality of root axes, and (e) the plasticity of these processes in response to environmental conditions such as soil strength, nutrient availability, water status, and oxygen status.

If we had a sound physiological understanding of these processes, they could be integrated into an understanding of root architecture as an aggregate trait. The best understood and researched subject among these is root gravitropism, which still enjoys debate and has unresolved details but about which an impressive physiological literature has been established, dating back to early observations of Darwin (Evans, 1991). A limitation to this research from the point of view of root architecture is that it deals predominately with short-term responses of gravistimulated primary roots of seedlings, whereas significant architectural features of root systems arise from the diverse gravitropic reactions of roots of different ages and classes as they mature.

Running a distant second to gravitropism as a research subject is the extension of root axes. The development of kinematics as an analytical context for root extension by Silk and colleagues has stimulated significant progress in understanding the growth dynamics of root axes (see refs. cited above). An outstanding example is the work by Sharp and colleagues on how water stress affects root extension (e.g. Spollen and Sharp, 1991). Another promising development in this area is the use of *Arabidopsis* mutants to study the developmental morphology of root axes (Schiefelbein and Benfey, 1991). The combination of molecular and mathematical approaches to root extension should permit substantial progress in this area in the coming decade.

Lateral branching is more mysterious. Although adventitious rooting has received a fair amount of attention (Davis and Haissig, 1994), the initiation and development of lateral roots is a complex and poorly understood subject that is essential to the understanding of the physiological basis of root architecture (Charlton, 1991).

Programmed root senescence is receiving increasing attention from ecologists because of its importance in nutrient cycling in ecosystems (Hendrick and Pregitzer, 1993), and root cortical senescence is postulated to be important in the internal recycling of P in grasses (Robinson, 1990), but virtually nothing is known about it from a physiological perspective, in contrast to leaf senescence. This is an

important gap in understanding the architecture of perennial root systems, in which a substantial fraction of the fine roots are lost every year, but may be less important in annuals, in which programmed root death appears to be less common.

Finally, the physiological basis of the plasticity of root growth in response to environmental variables is very poorly understood, with the possible exception of root response to water deficit (see the work of Sharp and colleagues referenced above).

One approach to the physiology of root architecture is to strengthen research on these component subjects, especially lateral branching and environmental plasticity, and gradually piece together an understanding of how they are physiologically integrated in root architecture, which, as argued above, may be the trait of functional relevance for the whole plant. This process will probably naturally occur with time. A more direct approach would be to look for physiological traits that may serve to integrate the behavior of individual root axes in coordinated architectural patterns. For example, in bean, P stress causes rapid changes in root gravitropism, lateral branching, root extension rate, and root hair elongation, which result in a shallower, more profusely branched root system. These are all processes that are influenced by auxin and ethylene: in this case hormones could coordinate architectural changes at several levels of organization in the root system. An important conceptual question that would help distinguish the validity of this approach is whether root architecture is merely the aggregate of processes occurring independently in individual root axes or whether processes such as hormonal responses and carbohydrate status regulate root architecture through coordinated action on subprocesses in root axes or even in different parts of the root system.

Some challenges to the physiological study of root architecture are the geometric complexity of architectural traits, the probable physiological complexity of architectural traits (considering the complexity of each of the physiological components of architecture), and the complexity of the soil environment being studied or simulated. In this regard the continued development of models and mathematical tools such as fractal geometry may be important as quantitative summaries of architectural traits. The complexity of architectural traits may make quantitative genetics more fruitful than single-gene approaches emphasizing mutants (although see Zobel, 1991). The complexity of the soil environment is a serious methodological challenge to root researchers. Although simplified media are necessary for controlled studies, few physiological researchers pay sufficient attention to important features of the soil environment such as gas composition and realistic nutrient concentrations that may fundamentally influence root growth and architecture. Mycorrhizas are particularly interesting (or from an experimental viewpoint, problematic) from an architectural perspective, since most higher plants are mycorrhizal, mycorrhizal colonization alters root topology (Schellenbaum et al., 1991), and mycorrhizal hyphae could complement root architecture by exploring regions of soil not explored by the plant symbiont itself. For these reasons

a multidisciplinary approach may be particularly appropriate in studying root architecture.

CONCLUSION

There is increasing evidence that root architecture is a fundamental aspect of plant productivity, especially in the many environments characterized by low water and nutrient availability. Methodological progress in various fields has improved our ability to visualize, quantify, and conceptualize root architecture and its relationship to plant productivity. However, we still know very little of the physiological basis for architectural traits. Studies of gravitropism must begin to consider different root classes, and the processes governing lateral branching, environmental plasticity, and root senescence need more attention. Multidisciplinary research linking root architecture, plant adaptation to edaphic constraints, and specific physiological processes, especially those that may coordinate the responses of distinct root axes, may improve our understanding of this challenging and important problem.

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